ON THE ROCK-BORING BARNACLE, LITHOTRYA VALENTIANA

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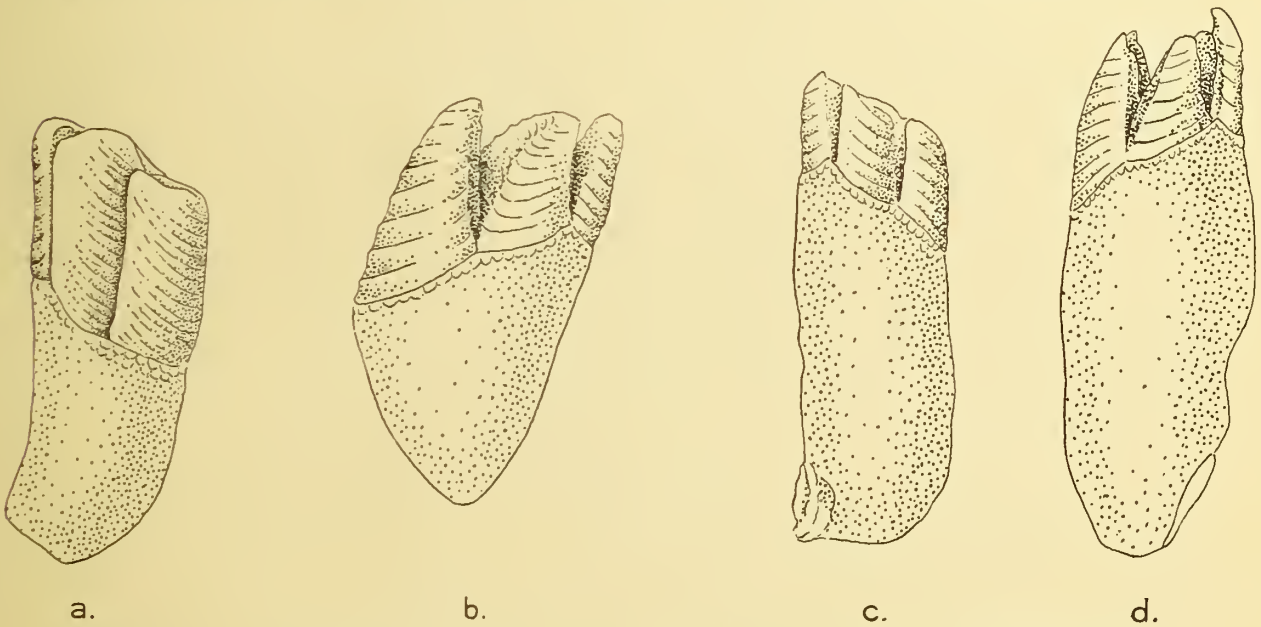
WITH SEVEN TEXT-FIGURES AND TWO PLATES.

THE original description of the genus *Lithotrya* was published by Sowerby in 1822. Since then eight species have been described. Of these *L. rhodiopus*, Darwin, is uncertain. Of the remaining seven, Seymour-Sewell (1926, p. 271 and p. 326), from a study of *L.*



TEXT-FIG. 1.—(*a*) Original figure of *Lithotrya truncata* (= *Anatifa truncata*); (*b*) Darwin's figure of *Lithotrya truncata*; (*c*) and (*d*) Gruvel's figures of *Lithotrya valentiana*. The outlines of these copies have been reproduced from the originals photographically.

nicobarica, Reinhardt, has recently grouped together five as "representatives of a single widely-distributed and somewhat variable species". If he is correct, these forms must all be described as *L. dorsalis*.

The two remaining species are *L. valentiana* and *L. truncata*. The former was described by Gray in 1825 as *Conchotrya valentiana*, and the latter by Quoy et Gaimard in 1834 as *Anatifa truncata*.

Gray's genus and species are defined as follows (1825, p. 102): "Shelly plates, five; two pair ventral, and one plate dorsal; peduncle —— ? Lives in holes in shells."

C. valentiana : " Shelly plates, thick, transversely lamellated. Inhabits Red Sea in the valves of *Ostrea Cucullata*, Born ; *Lord Valentia.*"

Quoy et Gaimard (1834, vol. iii, p. 636) describe their species thus : " Anatifa, subcylindrica, breviter pediculata, lutescens ; valvis crassis, rectis æqualibus, postice truncatis, transversis striatim ; pedunculo granulato."

No further account of these two forms was published until Darwin wrote his monograph on Cirripedes in 1851. Now it is obvious from the original diagnoses quoted above that at this time it was highly probable that the name *A. truncata* was synonymous with *C. valentiana*, and yet Darwin, who gave a full account of these two supposed species, made a sharp distinction between them. For his study* he had the original specimens of *C. valentiana*, but not those of *A. truncata*. However, a good figure had been published of the latter (Text-fig. 1*a* and Quoy et Gaimard, pl. 93, figs. 12–15). Now what Darwin figured under the name *Lithotrya valentiana* is, of course, correct, in the sense that the figures were drawn from the type-specimens, but also it is obvious that these figures depict a form closely similar to the figure of *A. truncata*. On the other hand, what he figures as *Lithotrya truncata* (Text-fig. 1*b*) is quite different from the original figure, and it is a mystery why Darwin made this decision. He lays great stress on the shape of the valves in describing the difference between the two forms, and yet the valves of his *L. truncata* are quite different from those shown in the original plate. They are not truncated in any way—they are all perfect, while in the original description it specifically states " valvis crassis . . . postice truncatis ". If, therefore, the shape of the valves was to be used as a diagnostic feature, Darwin had no right to name his specimen *L. truncata*. He should have made it the type of a new species, and at the same time he should have established the synonymy of the two forms and done away with the name *A. truncata*.

The matter is further complicated by the fact that Darwin did not publish a complete figure of the undisturbed valves of *L. valentiana* except for a vertical view of the capitulum. This was left to Gruvel, who, in 1902, published two figures under this name, one of which closely resembles the original picture of Quoy and Gaimard of *A. truncata*, while the other is quite different and similar to Darwin's *L. truncata* (Text-fig. 1, *c* and *d*).

Darwin distinguishes the two species almost entirely on the differences between the shapes of the valves, and of these, it is the terga that he stresses most. He states (1851, p. 372), referring to *L. valentiana*, " The valves . . . generally resemble those of *L. truncata* ; scarcely any appreciable difference can be detected in the scuta ". It cannot be maintained, however, that his figures support this statement. It is obvious, by comparing Plate VIII, fig. 5*a*, which is an inner view of the terga and scuta of *L. valentiana*, with Plate IX, fig. 1*b'*, *b* and *c*, which represent the same parts of *L. truncata*, that the scuta and terga are markedly different. Of the latter he states (p. 372) that there is " a fold or indentation . . . : this fold, . . . descends below the roughened knob at the upper angle of the carinal margin, which is not the case with the slight fold in the same place in *L. truncata* ", and this was the main, and probably the only, difference that he saw between the two species. Now I have been able to examine the two original specimens of *L. valentiana* on which Darwin worked, and while his description of the tergum

* Darwin's material is still in the collection of the British Museum (Natural History). Dr. I. Gordon in a letter states : " The two small dried specimens of *L. valentiana* described by Darwin are still in our collection, mounted on a small wooden block ; there is also a single specimen of *L. truncata* labelled by Darwin. The *L. valentiana* material must be Gray's original types (' Annals of Philosophy ', 1825 (2), x, p. 102), since, on the back of the block, is Gray's signature under the name ' *Conchotrya valentiana.*' "

applies to the larger specimen, it is not possible with any certainty to distinguish the limits of the fold to which he refers in the smaller. Moreover, even in the larger specimen the fold is certainly not as pronounced as drawn by Sowerby and figured by Darwin (1851, pl. viii, fig. 5*a*). In addition to this the shape of the terga in the two specimens differs to such an extent that it is difficult to imagine how Darwin could have based a specific difference on such a variable structure.

The only other point that I can find in Darwin's description that may have influenced him is that he states that the inner internal crest of the carina of *L. valentiana* is square " instead of round, as in *L. truncata* " (p. 372). Unfortunately, again the figures do not support this. In both cases they show a squarish crest rounded off at the edges.

Thus the position in which Darwin left matters in 1851 is, I submit, that (1) he described a new form as *Lithotrya truncata* when there was no evidence that it agreed with the original *Anatifa truncata* of Quoy and Gaimard, and (2) he described specific differences between his new *L. truncata* and the original *Conchotrya valentiana*, Gray, for the existence of which there was no real evidence.

The next authority to study these two species was Gruvel (1902). He described a new specific difference in the complete absence of the lateral plates in *L. valentiana*. Darwin, referring to this species, stated (p. 851, p. 373), " Latera lost; no doubt they were rudimentary ", while in *L. truncata* he stated that they were rudimentary (p. 369), and were " represented by mere stiles (likes strings of beads), and are even less in width than the rostrum " (p. 335). Gruvel, however, is much more emphatic. He states (1902, p. 250), " Malgré sa ressemblance avec *L. truncata*, il faut faire de *L. valentiana* une espèce différente, car un caractère essentiel les distingue ; c'est que dans la première il existe des plaques latérales, rudimentaires il est vrai, tandis qu'elles sont *absentes* dans la seconde ", and further, " Dans les deux échantillons examinés par Darwin, il n'y avait pas de plaques latérales et, étant donné le mauvais état de conservation dans lequel ils se trouvaient, l'illustre naturaliste avait pensé que si elles n'existaient pas, c'est qu'elles avaient peut-être disparu. Il n'en est rien.

" Si elles n'existent pas, c'est qu'il n'y en a pas. Je les ai vainement recherchées et cependant, mes échantillons étaient en excellent état ".

Now despite the fact that Darwin described these lateral plates as styliform in *L. truncata*, that is, latera quite unlike those of any other barnacle, and that Gruvel uses their presence and absence to distinguish two species, no one, as far as I can see, has ever figured them.

Unfortunately Gruvel describes the mouth-parts of specimens which he identifies as *L. valentiana* and states that the mandibles are asymmetrical. Certainly his figures (pl. xii, figs. 28 and 29) show a marked difference between the right and left mandible. Now he only had two specimens (p. 250), and it is not certain that he dissected both. Apart from this, since the original specimen of *L. valentiana* consisted of shells only and contained neither mouth-parts nor even body, he must have based his identification primarily on the valves ; and, as I have already stated, one of his figures closely resembles Darwin's figure of *L. valentiana*, and hence the original picture of *A. truncata*, while the other is much more like Darwin's picture of *L. truncata*. I cannot see, therefore, that Gruvel made out a case for the identification of his specimens as *L. valentiana*. In any case, he makes little reference to this asymmetry of the mandibles and stresses the absence of latera (p. 250).

Nilsson-Cantell (1921, p. 216), on the other hand, does not place much value on the

absence of latera as a specific difference. He states, " Dieser Unterschied scheint mir weniger wesentlich, da es auch oft bei Exemplaren von *L. truncata* schwer ist, die Lateralia zu finden ", and includes in his diagnosis of *L. truncata* (1921, p. 213), " Lateralia können mitunter fehlen ". Yet he also is prepared to accept the two species *truncata* and *valentiana*. He apparently used the mouth-parts for the identification of his specimen, for, referring to a new subspecies of *L. truncata*, he states (p. 217), " Auch kann ich die Tiere aus mehreren Gründen nicht zu *L. valentiana* rechnen, welche Art hinsichtlich der Mundteile abweicht . . . ". But here, again, there is a difficulty. For his comparison he must have accepted the only description of the mouth-parts of *L. valentiana*—that of Gruvel, which I have just mentioned—but his own description of the mandibles of *L. truncata* is quite different from the only previous description—that of Darwin (1851, p. 370). Darwin states that the mandibles have " eight pectinations between the first and second main teeth and three between the second and third teeth, . . . ". Nilsson-Cantell merely states (1921, p. 214), " Zwischen Zahn 1 und 2 ungefähr doppelt so viele kleine Zähne, als zwischen Zahn 2 und 3 "—and then figures a mandible with 14 pectinations in the first gap, instead of Darwin's 8, and 6 in the second instead of 3. Again I cannot see what real evidence Nilsson-Cantell was using when he decided that the form was *L. truncata* according either to Darwin or to the original account.

The position, therefore, as I see it at present, is that Darwin (1851), by not referring to the original figure of *A. truncata*, overlooked the fact that this form had previously been described as *C. valentiana*. Gruvel (1902) then described the absence of latera and the asymmetry of the mandibles in *L. valentiana*, when he had no evidence that his specimens belonged to this species rather than to Darwin's *L. truncata*. And finally, Nilsson-Cantell (1921) described the specific characters of the mandible of a form which he names *L. truncata* when this description disagrees with that of Darwin.

The Great Barrier Reef Collection consists of 30 complete specimens all collected in the Boulder Zone of Low Isles Reef. In general shape they show every gradation, from forms which closely resemble the original specimens of *C. valentiana* and the original figure of *A. truncata* (Plate I, fig. 1), to those which are similar to the form described by Darwin as *L. truncata* (Plate I, fig. 2, and Text-fig. 2). As regards the " latera ", these may be present or absent, and in two specimens, while the " lateral plate " is present on one side, it is absent on the other (Plate I, figs. 3 and 4). On these characters alone, therefore, there seems no reason why these specimens should not all be described as *Lithotrya valentiana*.

SIZE AND AGE.

The measurements of specimens Nos. 1–26 are given in Table I. As Seymour Sewell (1926, p. 273) points out with regard to his collection of *L. nicobarica*, the total length of the animal from the tip of the capitulum to the opposite end of the peduncle is of little significance owing to the varying state of contraction of the stalk. In addition, in *L. valentiana* the extreme variation in the degree to which the valves may be worn down makes this measurement useless for comparison. Thus one, specimen 3 (Plate I, fig. 2, and Text-fig. 2), has almost complete valves, while in another, specimen 7 (Plate I, fig. 5), the greater part of the valves has been worn away.

Using the width of the capitulum, that is, between carina and rostrum, the measurements group themselves roughly about a mean of 7·5 mm., with maximum numbers

TABLE I.

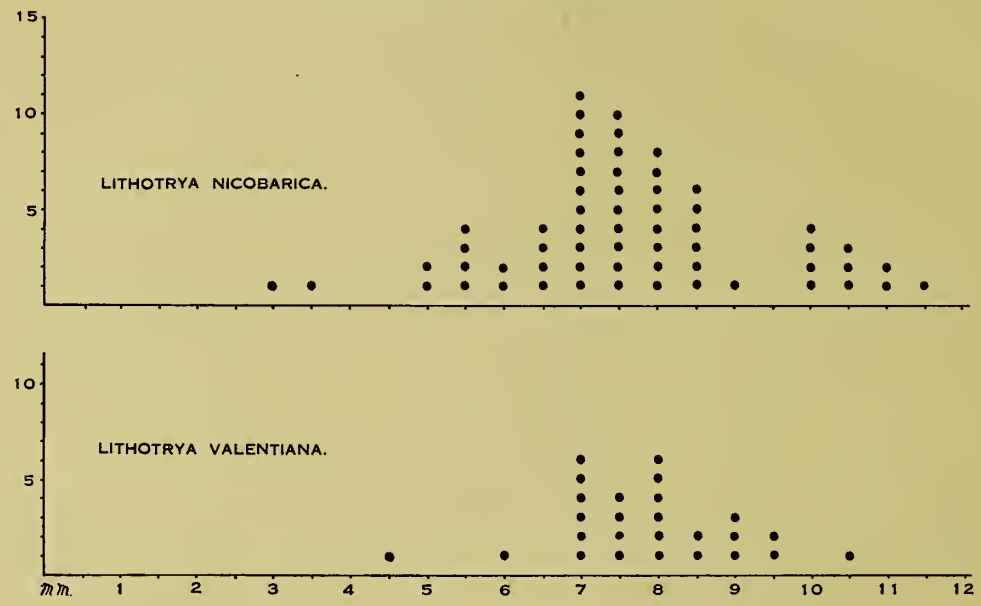
Specimen number.	Length (mm.).	Width at base of capitulum (mm.).	Scutum (mm.).	Carina (mm.).	Latera.* Left.	Latera.* Right.	Remarks.
1	20·5	8·0	10·0 9·0	5·0	56	3	Eroded more on one side than the other.
2	22·0	7·5	10·5 8·5	6·0	—	2	Lateral on one side only.
3	10·0	4·5	5·5	3·0	—	—	Latera absent. Typical *L. truncata* according to Darwin.
4	15·0	8·5	11·0	4·0	3 3	6 4	—
5	18·0	9·0	10·0	6·0	6(3)52	(1)9(2)32	On left side apical style is not the longest.
6	22·0	9·5	11·0	4·0	—	—	Very much overgrown. Latera, if any, obscured.
7	15·0	8·5	8·0 6·0	3·0	—	—	Latera absent.
8	23·0	9·0	11·0	6·0	6	3732	—
9	25·0	8·0	11·0	7·0	257	34	—
10	20·0	7·5	9·5	4·5	—	6	Latera on one side only.
11	20·0	7·0	10·0	4·0	2	—	Latera on one side only. Left side typical *Anatifa truncata*, Quoy et Gaimard.
12	17·5	9·0	8·0	3·0	—	—	Latera absent.
13	19·0	7·5	8·0	6·0	222	222	—
14	20·0	8·0	9·0	4·0	33	2	—
15	12·0†	7·0	9·0	4·5	23	4	
16	17·0†	7·0	6·0 7·0	4·0	22	4	—
17	18·0	8·0	7·0	5·0	23	62	—
18	22·0	10·5	12·0	7·5	222243	552	Apical styles curve inwards at tips between carina and terga
19	18·0	9·5	10·0	4·0	223	222	—
20	17·0	7·0	9·0	4·5	55	52	—
21	14·0	7·0	10·0	4·0	35	3	—
22	13·0	7·5	8·0	2·0	31	12	Apical styles not the longest.
23	16·0	8·0	9·0	4·0	224	2632	—
24	15·5	8·0	10·0	4·0	2	22	—
25	12·0	7·0	7·0	2·5	2	3	—
26	13·0	6·0	8·0	5·0	2	4	—

* Each figure represents the number of swellings in a lateral style. The figure in block type denotes the apical style; the others, those on either side. Where the figure is enclosed in brackets, this indicates that the style was obviously broken short.

† Shrivelled before fixation.

at 7·0 and 8·0 mm. Although only 26 specimens were available for measurement, and this was made to an approximate accuracy of 0·5 mm., the results are the same as those obtained by Sewell for *L. nicobarica* (Table II). Sewell, however, deduces from his measurements that the individuals show a grouping with four year-stages. His first-year group consists of 2 individuals with minimum size 3 mm.; second-year, 8, with minimum size 5·0 mm.; third-year, 39, with minimum size 6·5; and the fourth-year, 10, with minimum size 10·0 mm. Now his smallest specimen, from the point of view of collecting, was relatively large, so that there is no reason to assume that they were much more difficult to find than the larger. Also as he states (1926, p. 272), the animals occurred in groups in the rocks which were presumably broken open and carefully searched. It is to be deduced,

TABLE II.—*Showing Measurements of 60 Individuals of* Lithotrya nicobarica *and 26 Individuals of* L. valentiana.



therefore, that the collection represented fairly all sizes of individual present in the rock. Further, *Lithotrya* has no asexual method of reproduction. Under these conditions surely the first-year group must be larger than that of succeeding years—or rather, since we know nothing about the relative intensity of spawning in the years immediately preceding 1925, when the specimens were collected, we must assume this to have been approximately the same year by year, and hence the second and later year-groups must represent those that survive from preceding years. In other words, the first-year group must be the largest.

Sewell's figures for *L. nicobarica* and those now published for *L. valentiana* suggest merely that the two species grow to a size of at least 7 mm. diameter between the spawning time and the time when they were collected—10th April, *L. nicobarica*, and 31st May, *L. valentiana*.

In both series there are individuals considerably larger than the average, and in the case of *L. nicobarica* they form a separated group. Since they are smaller in number than the main group, it is safe to deduce that they may represent a second year, or even an older group.

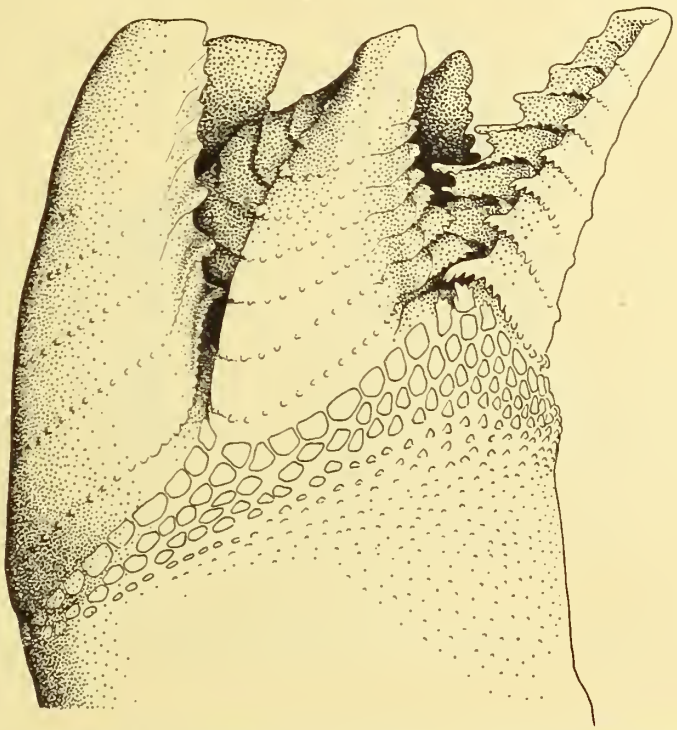
Also in both series there are small specimens separated considerably from the main group. In *L. valentiana* the one small specimen, No. 3, is by far the most perfect in the collection. It is possible that these small individuals, few in number, represent the products of a second subsidiary spawning period.

SHAPE OF VALVES.

It is not possible to publish illustrations of all the specimens of the collection, but it is clear, from the photographs and text-figures, that they vary markedly. Specimen 3 (Text-fig. 2; Plate I, fig. 2) corresponds closely to the form figured by Darwin as *L. truncata*, while specimen 11 (Plate I, figs. 1 and 6*c*) agrees with the original figure of *L.*

truncata and with the type-specimen of *L. valentiana*. In fact, it is possible in this small collection to copy any of the published figures of either species, and also to produce a complete series of intermediate forms.

Darwin. as I have pointed out (p. 2), used the shape of the individual valves as a specific criterion. In *L. valentiana*, in considering this point, it is clear that the apical margins cannot be used for comparison, for they are worn down to varying degrees. Thus, in Specimen 3 only the tips of the scuta were slightly worn away, while Specimen 11 had its valves so ground down as to appear as a transverse section in apical view (Plate I, fig. 6*c**). Specimen 7 (Plate I, fig. 5, and Text-fig. 3) was worn away to an even greater



TEXT-FIG. 2.—*L. valentiana*. Capitulum of Specimen 3 viewed from right side. Carina to right. × 16.

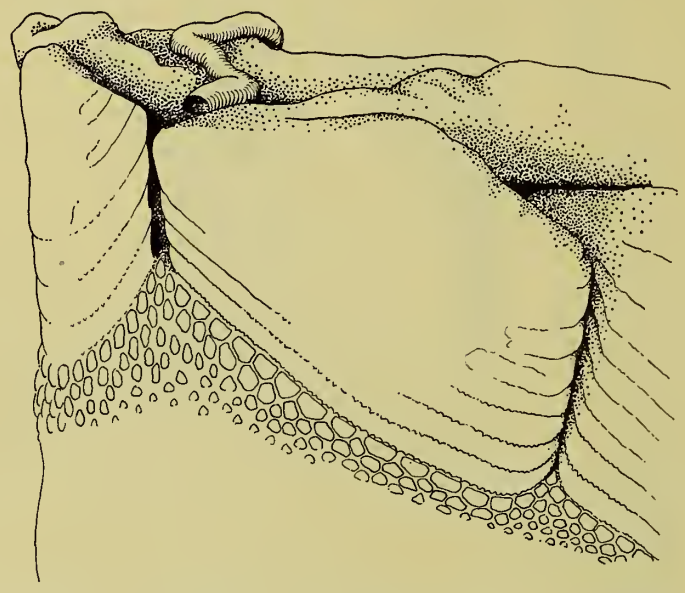
extent, and, further, as in several other specimens, it had been ground down unevenly, so that the valves of one side were definitely shorter than their fellows. Also, and in the majority of specimens, the apical surface was covered with a growth of sessile organisms which, in itself, made it difficult to see their actual margins.

The basal margins of the valves, on the other hand, should be unaffected by erosion. In Plate I, fig. 7*a*, *b*, *c*, are shown photographs of the inner view of the isolated valves of three specimens chosen at random from the collection. The isolated scuta, to the right of the figure, show marked differences. The ridge near the tergal margin which fits into the groove on the outer surface of the tergum (compare Plate I, fig. 6*b*, *c*) is massive in *c* and slender in *b*. The basal angle of the scuta also differs, but as the plates are curved

* In Darwin's monograph (1851, pl. viii, fig. 5*b*) there is a drawing by George Sowerby of the capitulum of *L. valentiana*—the type-specimen—seen vertically from above. From a study of the original specimen it is obvious that the scuta have been figured relatively too large and the terga too small. A correct drawing would correspond closely with Plate I, fig. 6*c*.

the photographs do not demonstrate this conclusively. Actually the angle of the scutum in *c* is more obtuse than that in either *a* or *b*.

It is the terga, however, that vary most, and as I have previously pointed out (p. 2) it was on the inner shape of the terga that Darwin based his distinctions between *L. truncata* and *L. valentiana*. The markedly different shape of the tergum shown in *c* from that in *a* can be seen from the isolated terga. But for comparison the best photographs are those to the left of the figure showing terga and scuta joined together in their natural position. From these it can be seen that, while in *a* the lower scutal margin of the tergum slopes continuously upwards away from the peduncle, in *c* it bends at an angle so as to run almost horizontally, while *b* shows an intermediate type.



TEXT-FIG. 3.—*L. valentiana*. Capitulum of Specimen 7 viewed from left side. Carina to left. The tube growing on the right tergum is that of a Vermetus-like Gastropod. × 11.

The carinae of the three specimens also show a graded series. The inner ridges on the carina *a* show the outline of a truncated cone, while those of *c* have the appearance of an inverted W.

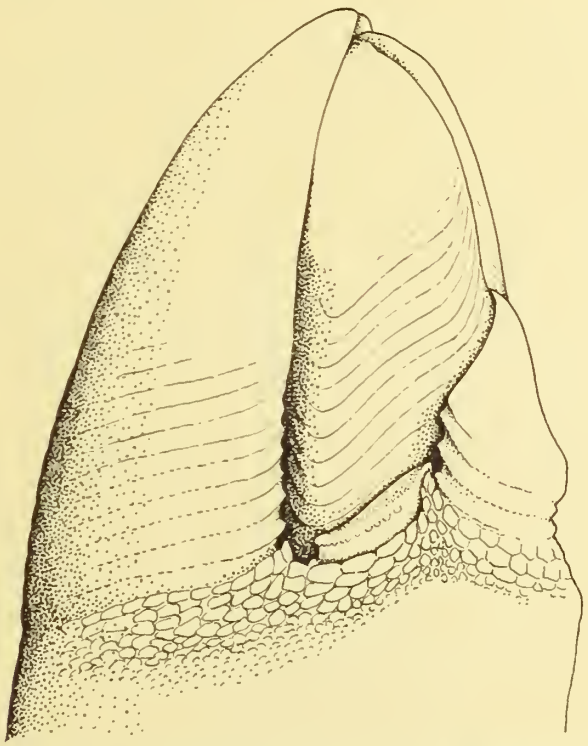
In only one specimen (No. 7) was the rostrum complete (Plate I, fig. 5); in all the others it was broken off near the base. It shows growth ridges laterally, corresponding to the ridges on the outer surface of the other valves, but as this specimen was so very much eroded, it was not possible to see whether the number of ridges on the rostrum agreed with that on the other valves. Six ridges can be counted and six at least on the other valves, but it is uncertain how many had been rubbed off the latter.

THE LATERA.

In all the species of *Lithotrya*, with the exception of *L. valentiana* and the form described by Darwin as *L. truncata*, the latera are well-marked plates and consist of one pair only. Darwin states (1851, p. 333), "I presume that they are homologous with the carinal latera in Scalpellum". They "are remarkable from being placed over the carinal

half of the terga, in an oblique position, parallel to the lower carinal margin of the terga " (1851, p. 335).

The capitulum thus consists, when the latera are present, of eight plates, and these are sharply separated from the peduncle. The line of demarcation is marked by a zone of scales, which diminish in size towards the base of the peduncle. Towards the capitulum they are arranged in rows following the basal margins of the capitular plates, but as they diminish towards the base, so their arrangement becomes irregular (Text-figs. 2, 3 and 4). It can be stated, therefore, that the capitulum is separated from the peduncle by a definite row of scales in the form of a girdle.



TEXT-FIG. 4.—*Lithotrya dorsalis*. From a specimen in the Manchester Museum. Viewed from right side. Carina to right. × 8.

This girdle does not run in a smooth curve round the peduncle from rostrum to carina; on either side it is bent upwards towards the tip of the capitulum, in two places forming angles. One of these is relatively small, and projects slightly between the base of the scutum and tergum. The other is much more marked, and projects between the carina and tergum (Text-fig. 3). But in *L. dorsalis* (Text-fig. 4), which can be taken as a species bearing typical latera, these plates overlie the carinal side of the terga, so that it can equally be stated that the girdle projects as an angle in between carina and latera. The important point is that there is no angle projecting between the lateral plate and the scutal part of the tergum. Thus, if the girdle were removed as a complete ring, then cut through near the rostrum and mounted flat, it would show four marked angles along its capitular margins. Two of these would be large and near the middle of the preparation, and would represent the carino-tergal angles, while on either side they would be flanked by the smaller tergo-scutal angles.

Now in four specimens of *L. valentiana* I have removed this girdle (Plate II, figs. 8*a*, *b*). To do this I place a very fine scalpel down the outer face of the scutum near the rostrum and underneath the girdle scales; then make an incision through the girdle at this point, and by lifting up one of the cut edges and using the scalpel it is possible to strip off the girdle complete. In each case, when the supposed latera were present, they came off with the girdle—they formed, in fact, the apical scales of the carino-tergal angle.

This fact alone suggests that in *L. valentiana* the real lateral plates are absent, and what have been taken as latera are simply modified scales of the girdle, which should be referred to as sublateral scales. There is further strong evidence to support this view.

In *L. dorsalis* (Text-fig. 4) the latera take no part in the formation of the girdle of scales, and are merely a pair of plates in the primary capitular series—carina, latera, terga, scuta and rostrum—which form a massive and compact capitulum quite distinct from the girdle. These plates, as in all other Cirripedes, are joined together very strongly by muscles or ligaments. In removing the girdle from *L. valentiana* it comes away quite easily until the rostrum is reached. For the sake of convenience it is best to attempt to remove this and mount it with the rest of the girdle, but because it is part of the capitular series and not of the girdle, it is attached very firmly to the scuta and is difficult to remove. It would be expected, therefore, that if the supposed latera were in fact the real latera, they, too, would be firmly attached to the adjacent plates—the carina and terga—and would be difficult to remove with the adjacent girdle scales. Actually they come away just as easily as the remainder of the girdle.

A more important point is the number of these supposed latera. Darwin in his description of the genus *Lithotrya* refers to one pair only (1851, p. 335), and in his description of the form which he diagnosed as *L. truncata* again he only refers to one " rudimentary " pair (1851, p. 369). In all the forms which Sewell has shown should be referred to as *L. dorsalis* (see p. 1), the single pair of latera are similar in pattern to the terga, which they overlie. The only difference lies in their small size and their shape. They are roughly triangular plates, with their bases coincident with the bases of the terga. Now in *L. valentiana* Darwin states (referring to his *L. truncata*) (1851, p. 369), that the latera are " rather smaller than the rostrum; almost cylindrical, slightly flattened, enlarged at each zone of growth, with one or two sharp teeth or spines on both faces; imperfectly calcified; . . . ". And again (1851, p. 335), " the latera are represented by mere stiles (like strings of beads), . . . ". Clearly, then, these latera are markedly different from those of *L. dorsalis*, and, in fact, as I have pointed out (p. 3), are unique as Cirripedian capitular plates. In Plate I, fig. 3, is a photograph of specimen No. 10, and this shows very clearly the lateral plate as a " mere stile "—" like a string of beads ". There can be no doubt therefore that the Great Barrier Reef Collection includes specimens showing the same type of latera as Darwin's *L. truncata*. To confirm this I inspected the original specimen and was able to make out the remains of these structures—at least on one side. Unfortunately the specimen has been coated with wax and is mounted on a board. On the exposed surface the lateral plate can be seen, but it has apparently been broken since Darwin examined it, as it is very short. It shows the moniliform swellings, but is too short to describe as a string of beads.

In the present collection some specimens show no lateral styles (Plate I, fig. 2). Others, such as specimen No. 10 (Plate I, figs. 3 and 4), show a lateral style on one side only. This fact alone is sufficient to establish the fact that they are not latera, but more

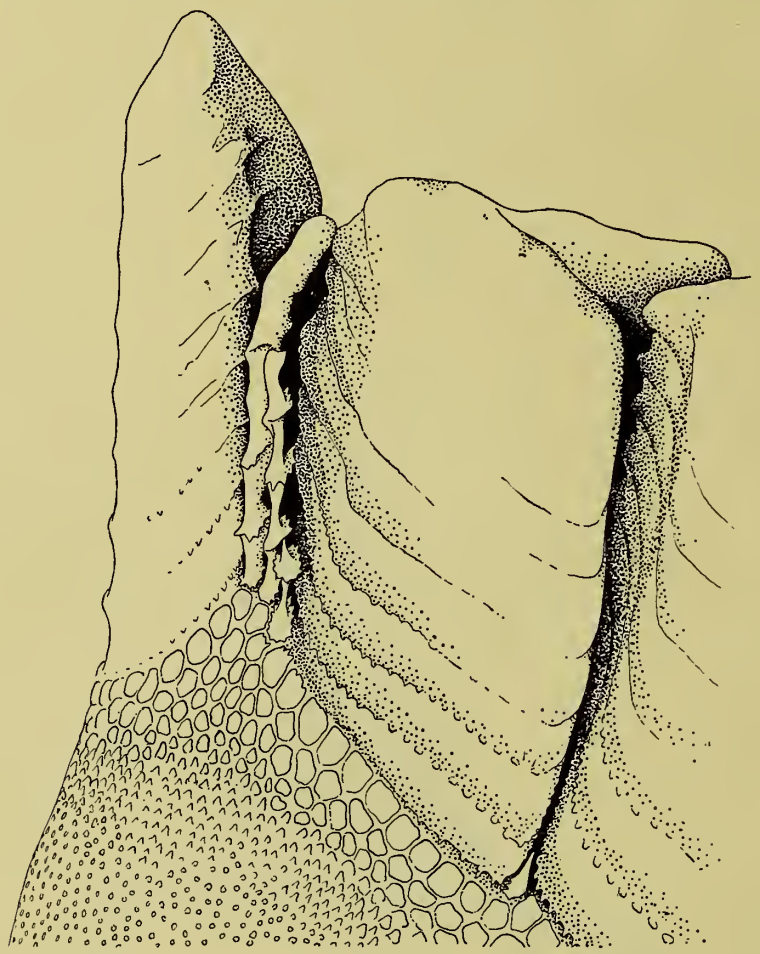
interesting is the fact that the majority show a group of such styles always in the typical position at the apex of the carino-tergal angle, but varying in number from one to six (specimen No. 18, see Table I). Now if it is assumed that, when only one pair of monili-

TEXT-FIG. 5.—*L. valentiana.* Left carino-tergal angle of girdle of Specimen 1. × 34.

form lateral styles is present, these are homologous with the lateral plates of *L. dorsalis*, then this argument fails in those specimens where there are more than one pair.

The shape, and more especially the sculpturing on the moniliform swellings of the styles, gives further evidence that they are related to the scales rather than to the plates.

Text-fig. 5 shows the left-hand carino-tergal angle of the girdle of specimen 1. There are two styles, of which the longer grows out of the apical scale. Counting the basal scale as the first zone of growth it shows markedly six distinct zones, while its neighbour shows five. The more distal swellings are indistinct. They have obviously been worn away in the same way as the more apical growth-ridges in the capitular plates and, in addition, are overgrown by a mat of algae and polyzoa. However, the first swelling above the base on the longer style shows clearly the same shape and sculpturing as the basal scale itself.



TEXT-FIG. 6.—*L. valentiana*. Capitulum of Specimen 9 showing details of left carino-tergal and tergo-scutal angles. × 12.

It has the form of an oblique shelf set at the same angle on the style as the base, and with its margins produced into sharp points in the same manner.

The left-hand aspect of Specimen 9 is shown in Text-fig. 6. There are three sub-lateral styles. The apical style shows six or seven swellings, of which the lower three show the sculpturing of the scales ; the adjacent style shows five swellings, all of which, except the apical, show the toothed flange, while the third style shows only two swellings, but these show even more clearly the similarity between the swellings and the girdle scales.

All the scales of the peduncle, even the smallest, contain a single minute central canal supposed to contain a nerve (Gruvel, 1905, p. 359). The capitular plates, on the other

hand, are penetrated by many such canals and, further, in sections of the decalcified plates, they appear to be arranged in rows, as if a new row were added at each growth zone. Now in the sublateral styles of Specimen 16 (Plate II. fig. 8*c*), which bear only two or three swellings, a single canal can be seen running the length of the style.

FORMATION OF SUBLATERAL STYLES.

Darwin (1851. pp. 61 and 336) has described the act of moulting in the genus *Lithotrya*, and Sewell (1926. p. 273) has recently published a concise summary of the process. The characteristic feature is that at each moult the cuticular covering of the peduncle is cast off, while that of the capitular plates remains. Immediately after each ecdysis the capitular plates grow downwards towards the peduncle, adding a new zone to their lower margins. As the animal continues to grow the plates thus become scarred with a series of ridges, each ridge recording a moult.

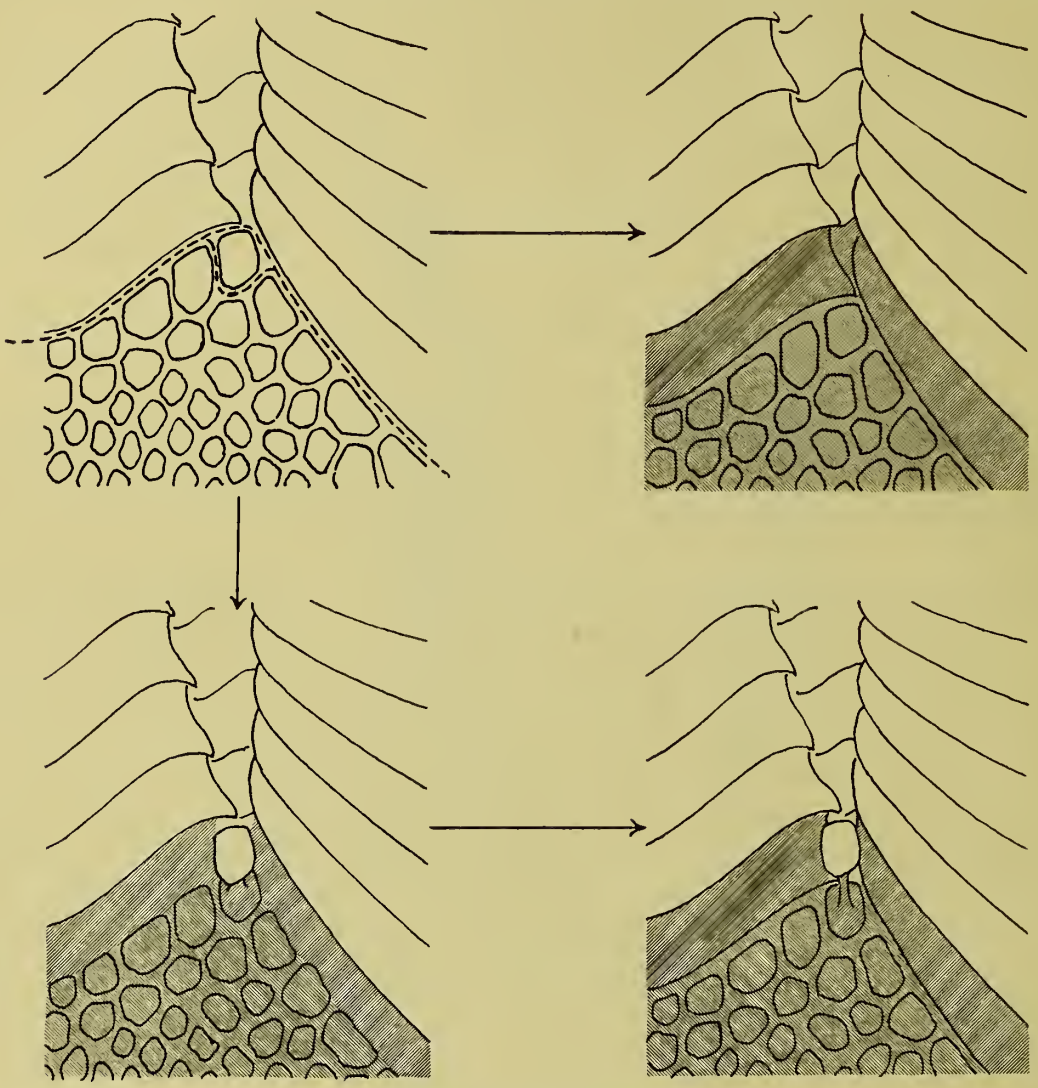
After each moult a new cuticle hardens over the peduncle, but also over the new zone on the capitular plates, and joins on to the old capitular cuticle, so that the whole body is covered with a continuous cuticular covering.

Clearly, at each moult this continuous cuticle must split along a line which separates capitulum from peduncle, that is, along the upper edge of the girdle (Text-fig. 7). The specimens in this collection I consider indicate that the presence or absence of sublateral styles depends on a slight variation in the course of this split.

When the capitular plates add on their new growth it can be said that in so doing they push the girdle downwards to a distance equal to their growth zone. As the new calcareous laminae and cuticular coverings are added on the lower margin of the plate, so, of necessity, must the girdle scales be forced away from the older parts of the capitulum.

Now, in those specimens, *e. g.* No. 3 and No. 10 (left side), where there are no sublateral styles, the exuvial split follows accurately the capitular margins of the girdle. In the other specimens I suggest that the split, instead of passing over the capitular side of the sublateral scales at the apex of the carino-tergal angle, passes along their peduncular margins (Text-fig. 7). This would result in these apical scales remaining connected to the capitular plates by the covering of cuticle—or, more accurately, the cuticular covering of the scales would remain in connection with the cuticle of the capitulum, for the exuvial split concerns the cuticle only and not the underlying tissues. In any scale or plate we can consider the external cuticle, covering the underlying sheet of ectoderm, which may be termed the centre. At ecdysis each scale centre loses its cuticular covering and forms a new one, while each plate-centre retains its cuticle, and forms additional cuticle to cover its new growth. In the case where, as I have suggested, the exuvial split passes along the peduncular margin of the apical girdle scales, the cuticle remains in contact with the capitulum, while the centres remain in their normal position in regard to the other scales. Hence, as the new growth is added to the capitular plates, the centres of these apical scales will be pushed away from their cuticle. But all the time, during this process, the scale centres will be secreting their new cuticle, so that at the end of the growth period the old cuticle of the scale will remain in its original position relative to the old cuticle of the capitulum, and at the same time connected by a *cuticular* connection to the new cuticle of the scale. The growth of the plate centres and of their overlying cuticle is neither continuous nor uniform. Sections show that the new calcareous growth added is not

homogeneous, but in the form of laminae, and this is reflected into the cuticle. At the beginning of each growth period, and almost to the end, thin uniform laminae of calcareous matter and of chitin are deposited. At the end, however, the massive layer is formed bearing the elaborate sculpturing which makes the edge of the growth zone so conspicuous. This same process, I suggest, occurs when the cuticle of the apical scales remains



Text-fig. 7.—Diagram illustrating suggestion as to formation of moniliform sub-lateral scales in *L. valentiana*. In the upper left-hand figure the dotted line represents the positions of the exuvial split. When the split passes above the apical scale of the girdle, it leads to the absence of " lateral " (top right), and when below, to their presence (bottom right).

attached to the capitular cuticle. At first, as the cuticle of the scale is pulled away from its underlying scale-centre, thin uniform laminae of chitin are deposited (Plate II, fig. 8*d*), but at the end of the growth-period the thick sculptured layer of chitin is deposited. The result will be that the old cuticular scale will be carried upward in a capitular direction, and at the same time will remain connected with the new sculptured cuticle by a stalk. If this process is repeated at each ecdysis, it will result in a styliform scale bearing

sculptured swellings at intervals, each swelling representing the cuticular covering of an apical scale that has been dragged away from the peduncle during the growth periods.

If my suggestion is correct, then it follows the distance between the moniliform swellings on the sublateral styles should be equal to the distance between the growth-zones on the capitular plates. The photographs and figures show that this is so. A more important result, however, is that the styles should be entirely cuticular. Darwin (1851, pp. 335 and 369) states that they are " imperfectly calcified ". In Specimens 16 and 13 (Plate II, fig. 9), where there are three sublateral scales, each of a simple, dumb-bell shape, it can be seen, even in the whole specimens, that they consist entirely of a yellow-brown transparent chitin and contain no opaque calcareous centre. In the girdles which I have mounted it can be seen that the lower parts of the styles, which are still clear and not overgrown by polyzoa, etc., consist largely, if not entirely, of chitin. They clear well in euparal, but may retain a dark central mass in the swellings. I believe that these dark zones do not represent calcified matter, but simply internal zones that have not dehydrated and so remain opaque in euparal. The calcareous centres of the peduncular scales become relatively transparent, so that if these opaque zones in the styles represented such centres, they, too, should clear.

I consider, therefore, that the so-called latera are really cuticular structures formed by the intermittent growth of the cuticle covering sublateral scales, and that this growth parallels the growth of cuticle on the capitular plates. Whether or not such sublateral styles shall occur depends, I have suggested, on whether the exuvial split in the cuticle occurs below or above the scales. There is another factor, however, which determines whether the styles once formed shall remain or be cut off at their base, and that is the sculpturing of the inner surface of the carina.

In Specimen 3 (Plate I, fig. 2, Text-fig. 2) the inner margin of the carina can be seen produced into beautiful sculptured ridges projecting in a rostral direction. Each ridge, of course, records the outgrowth at the end of a growth-period. Now, at the apex of the carino-tergal angle the lowest ridge projects over the apical scale like a hood. Clearly, then, in this specimen it would not be possible for a sublateral style to occur. The space which should be occupied by the style is already occupied by the inner carinal ridges. And further, if, as I suggested, the exuvial split did pass underneath the apical scale, so that this was carried upwards during the growth period, then at the end of this period, when the ridge grew out from the inner surface of the carina, it would push against and snap off the growing style at its narrowest part.

However, provided the exuvial split occurred in the right place, there is no reason why the scale to the immediate left of the apical scale should not form a style. This, by its upgrowth, would miss the carinal ridges. Although this has not occurred in Specimen 3, there are several specimens in the collection which indicate that this scale and not the apical formed the sublateral style. Thus the single sublateral style which occurs on the right side of Specimen 10 (Plate I, fig. 3) is not an outgrowth of the apical scale, but of the scale next to it on its rostral side. The left side of this same specimen (Plate I, fig. 4) also suggests that here there were originally two styles, one on the apical scale and the other rostral to it, but that these have been broken off by the overhanging carinal ridge. From the photo it can be seen that these are dark and translucent, while the surrounding scales are white and opaque. They are clearly covered with a thicker layer of cuticle than the other peduncular scales.

Specimen 3 is the smallest, and presumably the youngest, in the collection. Its sculptured ridges are more pronounced than in any of the others. This may be a normal variation, but also, I think, it may represent a growth character. As the animals become older so their growth ridges become relatively smaller. If this is so, then in an animal with a tendency to produce sublateral styles, at first, when the carinal ridges are large the apical scale may be unable to form a style, while that rostral to it is free to do so. Later, when the carinal ridges are less marked, the apical scale may find no hindrance in growing into a style. In this case there would be a group of at least two styles, of which the longest would not be the apical, but that rostral to it. This is the condition in specimens 5 and 22 (Table I).

Another factor which determines the occurrence of sublateral styles is simply whether or not there is room for them. If the carina and terga are too close together, then the styles, even if formed, cannot persist. This is probably the normal state of affairs in the tergo-scutal angle, where no styles have ever been recorded. In Specimen 13 (Plate II, fig. 9) the apical scale of this angle can be seen as a narrow triangle projecting up into the tergo-scutal junction. It is probable that at exuviation the split passes underneath this narrow apical scale, but no style is formed, simply because the terga and scuta are always very close together.

There are two abnormal specimens in the collection which, I think, support my suggestion that the position of the exuvial split may vary. In Specimen 15 two cuticular scales were adhering to the capitular cuticle in the lowest groove of the left tergum. Clearly in this case at the last ecdysis the exuvial split had passed round their lower peduncular margins. If they had remained in contact with their underlying centres they would have given rise to styles in this abnormal position. They were, however, only slightly adherent, and came off at once on brushing.

In Specimen 8 (Plate II, fig. 10) a large piece of the girdle covering the tergo-scutal angle has become detached from the cuticle on its peduncular side. The growth of the cuticle on the capitular plates corresponding to its upper margin has been inhibited, possibly due to the tubicolous animal which can be seen in this region. The split along its lower side, however, indicates that at the last ecdysis the exuvial split corresponded with it, but in this case the split must have extended to the deeper layers, including the scale centres.

CIRRI AND MANDIBLES.

The specimens in the collection showed such marked variability in other characters that I did not consider it advisable to dissect more than a few to study the variation in the jointing of the limbs and the pectinations on the mandibles. The results of such a study of four specimens are given in the following table for comparison with Nilsson-Cantell's figures (1921, p. 214) :

TABLE III.

	Cirri: Number of segments.												Caudal appendages.		Mandible: teeth between cusps.	
	I.		II.		III.		IV.		V.		VI.					
	A.	P.	A.	P.	A.	P.	A.	P.	A.	P.	A.	P.	Right.	Left.	1–2.	2–3.
Specimen 1	9	10	15	17	17	20	21	22	23	22	23	23	12	10	12	7
Specimen 2, left	10	9	13	14	16	17	20	18	20	21	20	12*	10	10	12	7
Specimen 5	9	11	17	17	17	18	20	21	21	23	21	21	9	9	16	6
Specimen 16	7	9	11	16	15	19	20	15*	20	24	21	23	10	10	11	6

* Incomplete.

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DESCRIPTION OF PLATE I.

Lithotrya valentiana.

Fig. 1.—Specimen 11. Typical *Anatifa truncata*, Quoy et Gaimard. × 14.

Fig. 2.—Specimen 3. *L. truncata* according to Darwin. × 7.

Fig. 3.—Specimen 10. Right side—" latera " present. × 7.

Fig. 4.—Specimen 10. Left side—" latera " absent. × 7.

Fig. 5.—Specimen 7. Rostral view showing complete rostrum. × 6·5.

Fig. 6.—Apical views showing varying degree of erosion of capitular plates (*a*) specimen 3, (*b*) specimen 8, (*c*) specimen 11. × 6·5.

Fig. 7.—Isolated valves—from left to right—left scutum and tergum, carina, right tergum, right scutum. (*a*) specimen 5, (*b*) specimen 1 (*c*) specimen 2. × 6.

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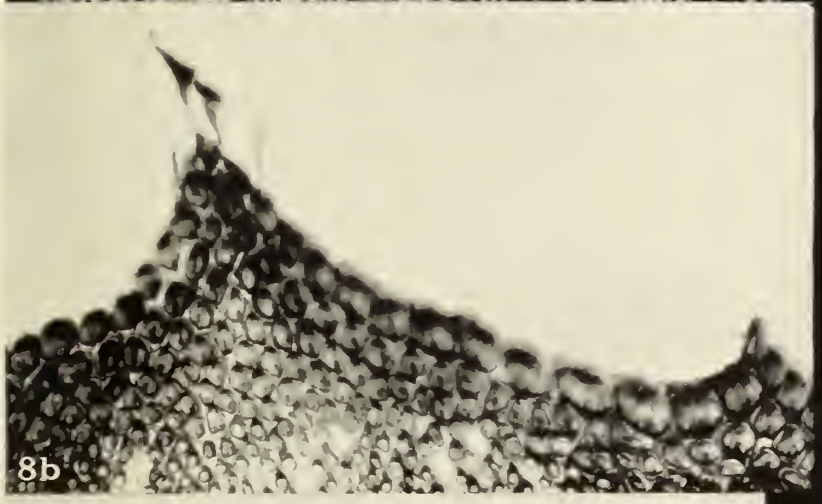
DESCRIPTION OF PLATE II.

Lithotrya valentiana.

Fig. 8.—Girdles. (*a*) Carino-tergal angles of specimen 14. × 36. (*b*) Left carino-tergal and tergo-scutal angles of specimen 16. × 36. (*c*) Sub-lateral scales (" latera ") of specimen 14. × 100. (*d*) Sub-lateral scales (" latera ") of specimen 16. × 100.

Fig. 9.—Specimen 13. Showing sub-lateral scale in tergo-scutal angle, and three chitinous sub-lateral scales (" latera ") in carino-tergal angle. × 7.

Fig. 10.—Specimen 8. Showing indications of abnormal exuvial split. × 5.



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